Plant Community Response to Thinning and Repeated Fire in
a Sierra Nevada Mixed-Conifer Forest Understory

By

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Abstract

Fire suppression in the western United States has significantly altered forest composition and structure, resulting in higher risk from fire and large-scale drought and bark beetle events. Mechanical thinning and prescribed fire are common treatments designed to reduce the risk of high severity fire, but few studies to date have tracked changes over longer time scales and with repeated fire application that emulates historic fire regimes. We evaluate changes in understory plant community diversity and composition and environmental characteristics over two decades following a factorial field experiment that crosses thinning and two applications of prescribed fire at the Teakettle Experimental Forest (TEF) in the southern Sierra Nevada. We compare experimental fuels treatments against nearby mixed-conifer forests with active fire regimes in Yosemite and Kings Canyon National Parks. This study points to key differences in how thinning and prescribed fire treatments affect plant understory diversity. Although local understory plant richness initially increased most following thinning combined with prescribed fire, this fuels reduction treatment did not generate understory communities similar to those in reference old-growth, mixed-conifer forests with frequent, low severity fire regimes. Intense growth of shrubs after thinning followed by fire resulted in low understory evenness and beta diversity over time, which a secondary burn treatment did not alter. In contrast, burning without

thinning retained a more heterogeneous understory over time and, at least in the two years following the second burn treatment, has responded to multiple burns with high understory richness and evenness, conditions more similar to reference forest understories. Our results suggest management treatments may need to focus on creating heterogeneity not only in burn effects but also in environmental conditions to foster diverse forest understories and limit shrub cover.

1. Introduction

Fire suppression in the western United States has significantly altered forest composition and structure, greatly increasing tree density– especially small trees – and homogenizing stand structure, wildlife habitat, and the understory environment (North et al. 2009, Safford and Stevens 2017). The resulting forests experience higher risk from fire (Koontz et al. 2020) and are less resilient to large-scale drought and bark beetle events (Fettig et al. 2019). Common fuels reductions treatments designed to increase forest resilience, such as mechanical thinning and prescribed fire, can effectively reduce wildfire severity under moderate temperature and humidity conditions (Safford et al. 2012). However, we know less about how these fuel treatments affect the broader plant community over time. Without treatments, both fire-suppressed and post-high severity fire states have resulted in homogenized forest understory microclimate (Ma et al. 2010), reducing understory plant diversity while significantly increasing shrub cover in the Sierra Nevada (Coppolleto et al. 2016). Maintaining understory plant diversity in western U.S. forests has important implications for regional biodiversity and ecosystem functions. In California over 50% of vascular plant species are found in the Sierra Nevada (Potter 1998), and within mixed-conifer forests most of the plant diversity is contained in the understory communities (Shevock 1996).

Greater fine-scale environmental heterogeneity in burned compared to thinned forests may increase plant biodiversity (Halpern and Spies 1995; McIver et al. 2012). For example, in the short-term (1-3 years after treatment), thinning without the use of prescribed fire can reduce understory cover and diversity due to increased cover of slash and litter on the forest floor (Wayman and North 2007). In contrast, a study of stands with various burn histories – but no thinning – over a 20 year period in Sequoia and Kings Canyon National Parks found that repeated use of low-intensity prescribed fire increased forest habitat heterogeneity, providing a gradient of resource conditions that contributed to restoring understory diversity (Webster and Halpern 2010). While several experiments have examined the short-term effects of thinning and prescribed fire together on understory plant diversity (Abella and Springer 2015), few studies to date have assessed these changes for the same plots over multiple decades and with repeated fire application.

In this study, we evaluate changes in understory plant diversity and composition over two decades following fuels reduction treatments at the Teakettle Experimental Forest (TEF) in 2000-2001, followed by a second prescribed fire in the burn treatments in 2017, and compare them against nearby mixed-conifer forests with active fire regimes in Yosemite and Kings Canyon National Parks. Our overall objective was to understand long-term understory response to common forest management treatments including second-entry prescribed fire. Specifically, we addressed four questions: 1) How does understory plant diversity respond over time after thinning and prescribed fire, and does this response differ after a second prescribed burn event relative to a single prescribed burn event? 2) How does understory plant community composition respond over time following treatments including a second prescribed burn? 3) What burn treatment characteristics and environmental factors influence response to these treatments? 4) How do post-treatment communities and environmental conditions compare with nearby mixed-conifer forests with active fire regimes? Understanding the long-term effects of fuels treatments on the forest understory can help researchers and foresters improve management practices to reduce wildfire severity while retaining the understory plant community's rich diversity and habitat heterogeneity.

2. Methods

2.1. Study Sites

2.1.1. Teakettle Experimental Forest

The Teakettle Experimental Forest (TEF) is an old-growth, mixed-conifer forest in the southern Sierra Nevada, located in the High Sierra Ranger District of Sierra National Forest (36°58'N, 119°2'W). The study area ranges from 1,880 to 2,485 m in elevation and is dominated by white fir (*Abies concolor*), red fir (*A. magnifica*), incense-cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), and sugar pine (*Pinus lambertiana*) in the overstory (North et al. 2002). Soils are predominantly poorly developed and granite-based Inceptisols and Entisols with a coarse, sandy-loam texture and very low clay content. The climate is typical of the southern Sierra Nevada with hot, dry summers and cool, moist winters. Precipitation averages 1,250 mm per year and falls mostly as snow between the months of Nov. and Apr. Air temperatures range from a summer mean of 17.1°C to a winter mean of 1.2°C. Fires historically occurred every 17 years on average until 1865, after which no fires larger than 3 ha occurred in TEF (Fiegener 2002; North et al. 2005). There is no history of significant logging prior to experimental thinning treatments, except for limited hazard tree and sugar pine removal during early white pine blister rust control efforts (North et al. 2002, Smith et al. 2005).

A long-term field experiment testing the effects of different combinations of burning and thinning treatments was established at TEF in 1998 Thinning treatments were: no thin, a thin of all trees between 25 and 75 cm diameter at breast height as decribed by Verner et al. (1992) (hereafter referred to as an understory thin), and a heavier thinning treatment cutting all trees >25 cm DBH but leaving 20 large (>75 cm) evenly spaced trees per hectare (hereafter overstory thin). Thinning treatments were crossed with prescribed burning and no prescribed burning for a full factorial design with 6 treatments. Each treatment was replicated in three 200 m x 200 m square plots (Figure). Burn treatments were thinned in 2000 and burned in 2001, and unburned treatments were thinned in 2001. Full initial treatment details can be found in North et al. (2002). Burn plots were re-burned in fall 2017, emulating the historic fire return interval of the site. Thinning treatments were randomly assigned, but for operational reasons, the burn treatments were applied to two clusters of adjacent plots.

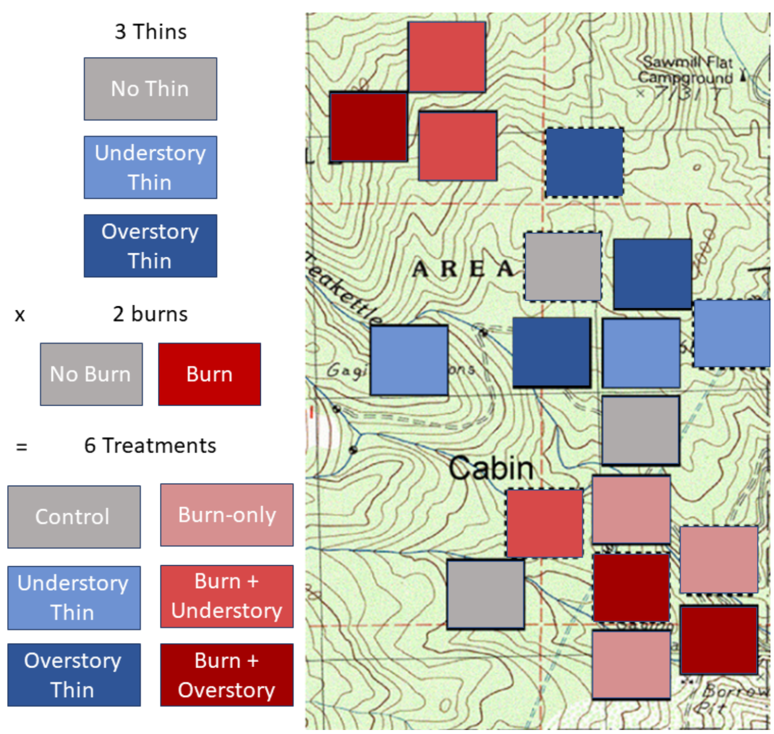


Figure 1. Map of the Teakettle Experimental Forest showing locations of square 4 ha plots for each treatment in the factorial experimental design.

2.1.2. Old-Growth Mixed-Conifer Reference Sites

Old-growth mixed-conifer forest sites with frequent, low-severity fire regimes (hereafter reference forests) in the central and southern Sierra Nevada were identified with similar forest type and topographic conditions to TEF. These sites were identified in ArcGIS 10.6 by overlapping the mixed conifer forest type in the CalVeg database (USDA Forest Service 2018), an elevation range of 1830 to 2286 m in the USGS National Elevation Dataset (USGS 2018), and an active fire regime consisting of at least three fires between 1960 and 2018 and at least one fire after 1990. Fire histories were determined using the CalFire Fire and Resource Assessment Program's Fire Perimeter database (CAL FIRE 2018) and identifying areas of low to moderate severity fire effects similar to historic fire regime conditions. Reference forest plots were selected based on having similar slope and aspect to TEF plots, no history of logging, geographic proximity to TEF, and multiple unique combinations of fires geographically close to each other. Plots were ground-truthed to confirm mixed-conifer forest overstory species composition similar to TEF. Three locations were selected based on the above criteria: Gin Flat (37°46' N, 119°46' W) and Frog Creek (37°58' N, 119°46' W) in Yosemite National Park, and Grant Grove (36°45' N, 118°58' W) in Kings Canyon National Park. Three plots representing unique combinations of fires were sampled in each location.

2.2. Experimental Structure and Field Data Collection

Data were collected in a nested structure within plots. At TEF, permanent sample locations called gridpoints (hereafter referred to as sub-plots) within each plot were mapped and marked using a surveyor's total station. Two replicates for each treatment had nine sub-plots on a 50 m by 50 m grid and one replicate was intensively sampled at 49 sub-plots on a 25 m by 25 m grid for a total of 402 sample points. For reference forest sites, data was collected at 15 sub-plots in each of the 9 plots, with 25 – 50 m spacing between sub-plots. All sub-plot centers were monumented to ensure repeated measures in the same precise locations.

2.2.1. Vegetation and Ground Cover

At each sub-plot, we recorded ocular percent cover estimates for each plant species within a 10 m^2 circular plot centered on the sub-plot. We collected unknown species outside of the plot (where possible) and identified them using the Jepson Manual (Baldwin et al. 2010). Species that could not be identified to species were identified to genus, and we identified plants within the order Poales to family. We also recorded ocular percent cover estimates for bare ground, rock, litter (<1 cm diameter), sticks (1 – 5 cm diameter), and coarse woody debris (>5cm diameter). We averaged litter depth at 3 random locations in each sub-plot. We estimated coarse woody debris cover in two categories: decay classes 1-3 and decay classes 4-5 (Maser et al. 1988). In years following burn treatments, we recorded ocular percent cover estimates for ash and char material to indicate fire extent and severity at each sub-plot. We collected vegetation and ground cover data in mid-June through early July, coincident with peak blooming period for the region in 1999, 2002, 2003, 2004, 2006, 2011, 2012, 2013, 2016, 2017, 2018, and 2019.

2.2.2. Environmental Data

We recorded latitude, longitude, slope, and aspect at each sub-plot. Aspect was transformed to a relative measure of heat load using the equation $(1-\cos[\Theta-45])/2$ where Θ is the azimuth measured from true north (Beers et al. 1966).

We sampled volumetric water content using a TDR (Time Domain Reflectometer) in the top 12 cm of soil at the same time as vegetation was sampled to assess shallow soil moisture. A Fieldscout TDR 100 probe was used to average 5 measurements in each sub-plot (at sub-plot center and 1 m in each cardinal direction). In 2018, TDR sampling locations were flagged in all sub-plots to ensure repeated sampling of the same soil columns. These methods were used in 2018 and 2019. From 1998-2017, data were collected using a TDR with permanent installed rods at a single location in each sub-plot assessing 0-15 cm and 15-40 cm of the same soil profile (Zald et al. 2008).

We estimated soil depth by pounding a rod into the soil in five randomly selected locations within 2 m of the sub-plot and taking the mean of the three greatest depths. We collected soil samples from nine sub-plots in each plot in 2003 and 2019 for nutrient and soil texture analysis. Three soil cores were taken to a depth of 30 cm with a 2 cm wide soil probe at approximately 75 cm from the sub-plot center at 0, 120, and 240-degree azimuths. In 2003, soil samples were split into 0-10 cm and 10 – 30 cm depths, and in 2019 the entire 0-30 cm depth was sampled as a single unit. When cores were not able to be taken to the full 30 cm depth, additional cores were collected from the plot until sufficient soil was collected to complete all analyses, and core depths recorded. Cores were combined in waterproof bags and kept on ice for up to 7 days. They were then air dried and analyzed by the UC Davis Analytical Laboratory for total carbon and nitrogen (AOAC-International, 1997), Bray phosphorus (the recommended method for low pH soils: Olsen and Sommers 1982), and particle size (Sheldrick and Wang 1993).

We assessed light availability at each sub-plot with hemispherical canopy photographs taken with a Sigma 4.5mm F2.8 EX DC HSM Circular Fisheye lens. All photographs were taken from the center of the sub-plot at breast height using a leveled tripod at dawn or dusk, with the top of the picture oriented to true north. Photographs were taken at the 402 sub-plots in TEF in 1999, 2002, and 2019, and at all 135 subplots in the reference forest plots in 2019.

2.3. Analyses

All data analysis was performed in R version 3.6.3 (R Core Team 2020), unless otherwise noted.

2.3.2. Plant Diversity and Cover

Plant diversity metrics were calculated using the vegan package in R (Oksanen et al. 2017). Local scale alpha richness, diversity (antilog Shannon-Wiener diversity index (Jost 2006), and evenness (diversity / richness), were calculated at each sub-plot in each year. Gamma richness and beta diversity (average Raup-Crick dissimilarity index (Raup and Crick 1979)) were calculated within each plot in each year. All diversity metrics were averaged within treatments for each year. Total plant cover, shrub species cover, herbaceous species cover, and graminoid species cover were also calculated for each sub-plot for each year and averaged across treatments. We then calculated the change in diversity and cover values from their pre-treatment values for each sub-plot by subtracting pretreatment values from each year's values.

Due to the non-normal distribution of plant diversity, cover, and environmental data, we used the non-parametric Kruskal-Wallis tests with Dunn's post-hoc tests to identify differences in conditions between treatments in different treatment years. We used Friedman's Tests with post-hoc Wilcoxon's tests to compare repeated measures of our response variables over time within treatments, with sub-plot as the grouping variable for repeated measures.

2.3.1. Hemispherical photographs

Hemispherical canopy photographs were corrected for exposure and analyzed for percent canopy cover and direct, diffuse, and total photosynthetically active photon flux density (PPFD) (μmol s^{-1} m^{-2}) using the Hemiphot.R package in R (ter Steege 2018). For a given sub-plot, PPFD is calculated from the latitude, elevation, and the tracking angle of the sun over the course of a year. We used PPFD values as an approximation of the relative difference in understory light conditions between sub-plots.

2.3.3. Modelling Treatment Effects on Understory Diversity

We fit multi-level Bayesian linear regression models using the brms package (Bürkner 2017) to compare effects of burn and thin treatment combinations on changes from pre-treatment values in local richness, evenness, and diversity following initial treatments in 2000 and 2001 and second burn treatments in 2017. In each model, we include random effects for plot and year, with fixed effects for thin treatments, number of burn events, and their interactions. We use weakly-informative regularizing priors to aid in model convergence and avoid biasing our posterior distribution towards extreme parameter values. To assess differing treatment effects over time, we compare models with and without linear and polynomial terms for time since disturbance. Joint posterior distributions were sampled using MCMC sampling with 3 chains of 2000 iterations, and 1000 warm-up samples. We diagnosed model convergence using trace plots and Gelman-Rubin diagnostic values < 1.01 for all model parameters. Burn and thin treatment effects on response variables were compared using pairwise contrasts of posterior samples of estimated marginal means with the emmeans package in R (Lenth 2020).

2.3.4. Ordination for multivariate community responses

We separated our data set into a plant community matrix and a matrix of environmental variables for ordination using the vegan package (Oksanen 2011). We excluded rare species (occurring in less than 1% of sub-plot-year combinations), and used log-transformed cover values of the remaining 34 species to create a distance matrix using Bray-Curtis dissimilarity values and conduct ordination using NMDS (non-metric multi-dimensional scaling) with two axes. We calculated environmental loadings for each environmental variable using the envfit function with 999 permutations. We used the betadisper function to analyze multivariate homogeneity of group dispersion for plant communities in each treatment-year combination, with Tukey's post hoc analysis to determine which treatment years were significantly more homogenous (having more similar species present in similar abundances to one another) or heterogenous.

2.3.5. Modelling Environmental Variable Impacts on Understory Diversity

We fit multi-level linear regression models using the lme4 package (Bates et al. 2015) to determine the effects of environmental conditions on local richness, evenness, and diversity using vegetation and environmental data from 1999, 2003, 2016, and 2019 (pre- and post-treatment for initial thinning and both prescribed burn events). We include in each model random effects for plot and year, with fixed effects for average litter depth, percent cover of bare soil, shallow soil moisture (volumetric water content), total understory light availability (PPFD), as well as percent cover for dominant shrub species and interactions with shrub cover. We calculate marginal effects for each predictor variable using the ggeffects package in R (Lüdecke 2018).

3. Results

3.1. Understory diversity following initial thin and burn treatment and second prescribed fire.

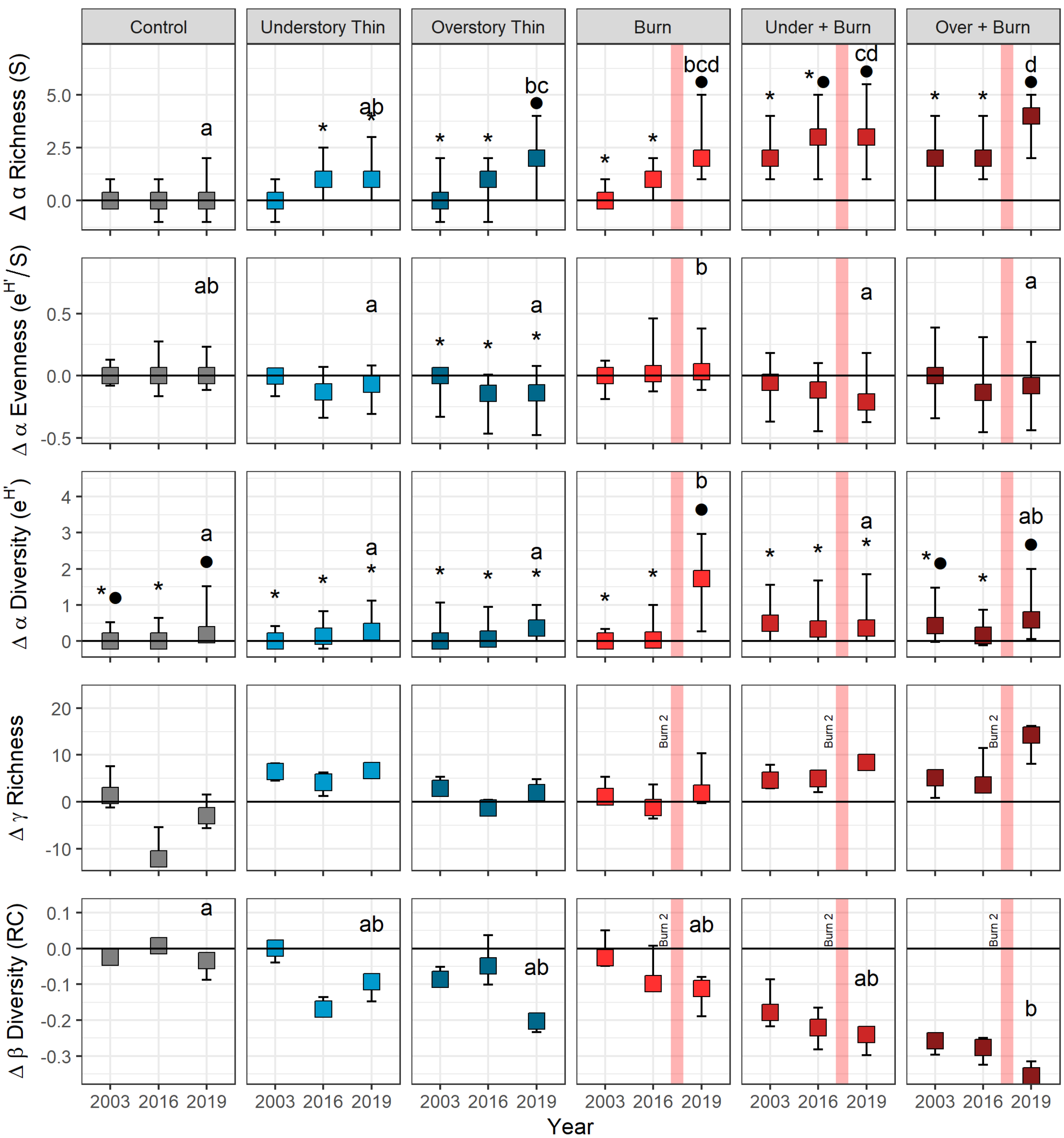


Figure 2. Change from pre-treatment levels 2 years after initial treatment, 15 years after initial treatment, and 2 years after second prescribed burn event for (from top to bottom) fine-scale richness, diversity, and evenness, and plot-scale richness, and beta diversity in the understory plant community. A value of zero indicates no change from pre-treatment conditions. Different letter superscripts within plots indicate significant differences across treatments in 2019 (Dunn's post hoc of the Kruskal-Wallis test, adjusted $p < 0.05$). Asterisk and black circle superscripts within plots indicate significant differences between years within a treatment, and either symbol indicates a significant difference from initial conditions in 1999 (Wilcoxon's post hoc of the Friedman test, adjusted $p < 0.05$). Points represent median values and ranges represent the 25th and 75th percentile values.

Thin and burn treatment effects on understory plant diversity over time differ depending on the diversity metric (Figure 2). At the local scale, initial thin-burn treatments increased sub-plot richness the most (adding 2-3 species, on average), and that increase remained until the second burn. Thin-only and burn-only treatments did also eventually display a smaller increase. After the second burn, sub-plots in the burn-only and overstory thin-burn treatments significantly increased in local richness, but there was no significant increase in the understory thin-burn treatment.

Local diversity follows a similar pattern after the initial treatment, with the largest increase in the thin-burn treatments, and smaller increases in other treatments. Following the second burn, the burn-only treatment had a large increase in diversity (+1.2 effective species on average), with smaller but significant increases in the overstory thin-burn treatment.

Local evenness only slightly changed following initial treatments but declined over time in all treatments except for

At the plot level, no treatments decreased in species richness following initial treatment or secondary burning, and some increased richness slightly following treatments. However, there were no significant differences in richness between treatments within years, or within treatments between years. This is likely due to the small number of replicate plots in this field experiment ($n = 3$ plots for each treatment).

Beta diversity within plots did not show significant differences between treatments until 15 years following initial treatment. Time had a significant effect on beta diversity in the control and understory thin-burn treatment (Friedman's test, $n = 3$, $df = 3$, $p < 0.05$), but no pairwise comparisons between years were significant. Fifteen years after initial treatments, treatment had a significant effect on beta diversity (Kruskall-Wallis test, $n = 3$, $df = 5$, $p < 0.05$), and overstory thin-burn treatments had significantly lower beta diversity than the control following the second prescribed fire. There were no other significant differences in beta diversity between treatments within years, or within treatments between years, possibly due to the small number of replicate plots in this field experiment ($n = 3$ plots for each treatment). The burn-only treatment did not lose beta diversity until after the second burn treatment.

3.2. Understory community composition following initial thin and burn treatments and second prescribed fire

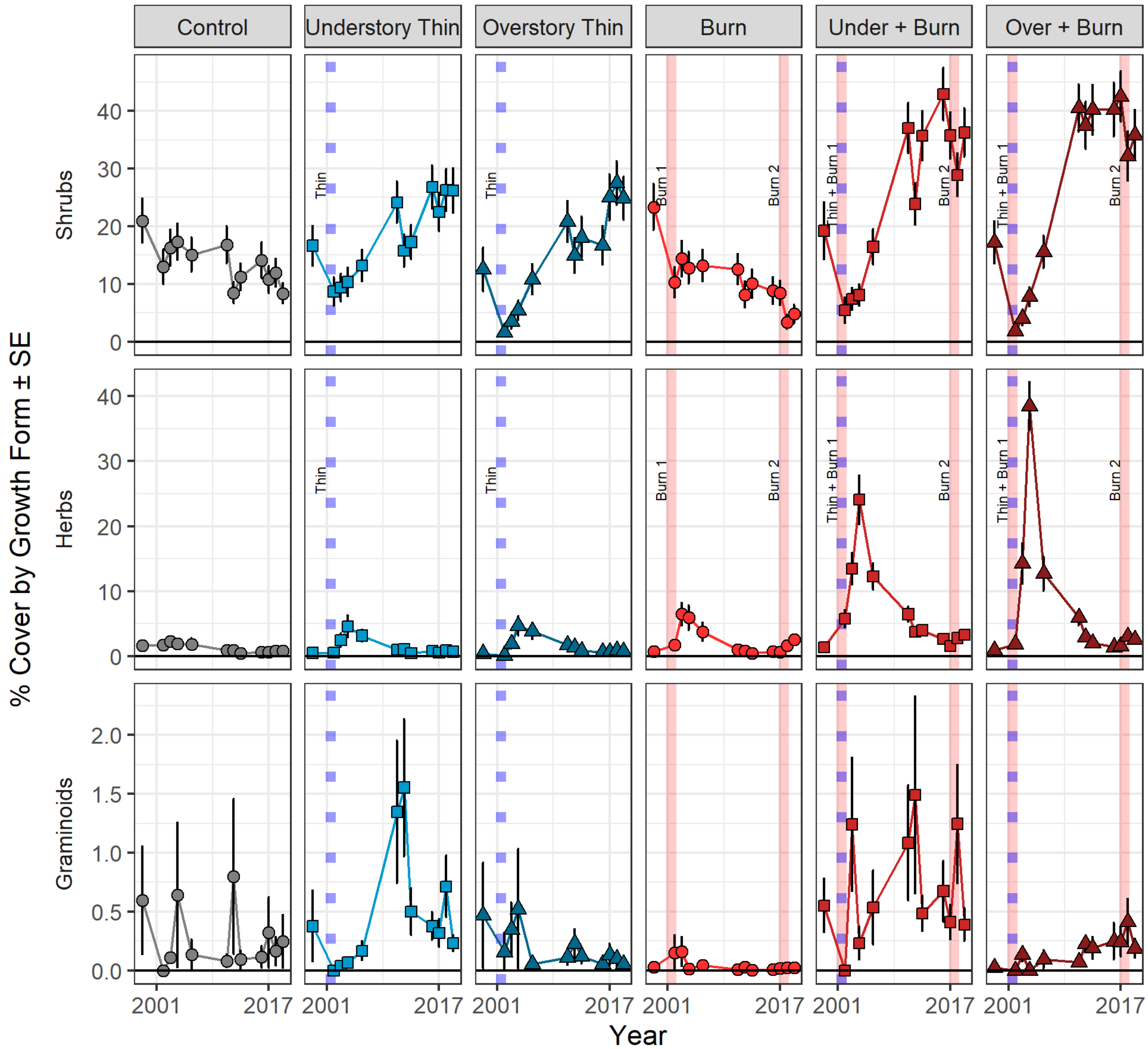
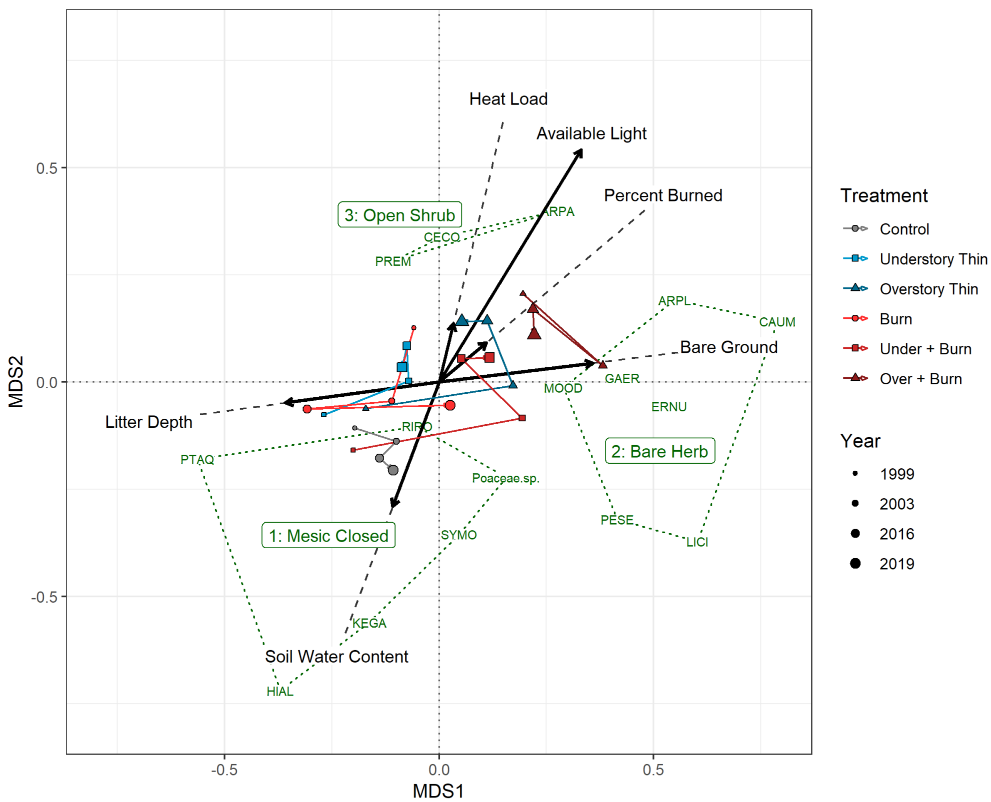


Figure 3. Plant cover by growth form over time. Points and ranges indicate mean percent cover ± standard error of (top to bottom) shrub species, herb species, and graminoid species from 1998 to 2017 across all treatments. Note different y axis scale for graminoids. Vertical

We found that total understory plant cover closely tracks shrub cover across treatments (Figure 3) as it comes to dominate the understory. Shrub cover initially decreased across all treatments, but increased dramatically over time in the thin-burn treatments, and to a lesser extent the thin-only treatments. The second burn did not reduce shrub cover significantly in any of the burn treatments after 2 years. Herbaceous cover increased briefly following the initial thin-burn treatments and to a lesser extent in burn-only and thin-only treatments. Following the second burn treatment, herbaceous plant cover did experience a small but significant increase in burn-only and overstory thin-burn treatments. Graminoid cover was low and highly variable within treatments.

A)


Heat Load
Available Light
Percent Burned
3: Open Shrub
ARPA
CECO
PREM
ARPL
CAUM
Bare Ground
GAER
MOOD
ERNU
2: Bare Herb
Litter Depth
RIFO
PTAQ
Poaceae.sp.
PESE
LICI
1: Mesic Closed
SYMO
KEGA
Soil Water Content
HIAL
MDS1
MDS2
Treatment
Control
Understory Thin
Overstory Thin
Burn
Under + Burn
Over + Burn
Year
1999
2003
2016
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B)

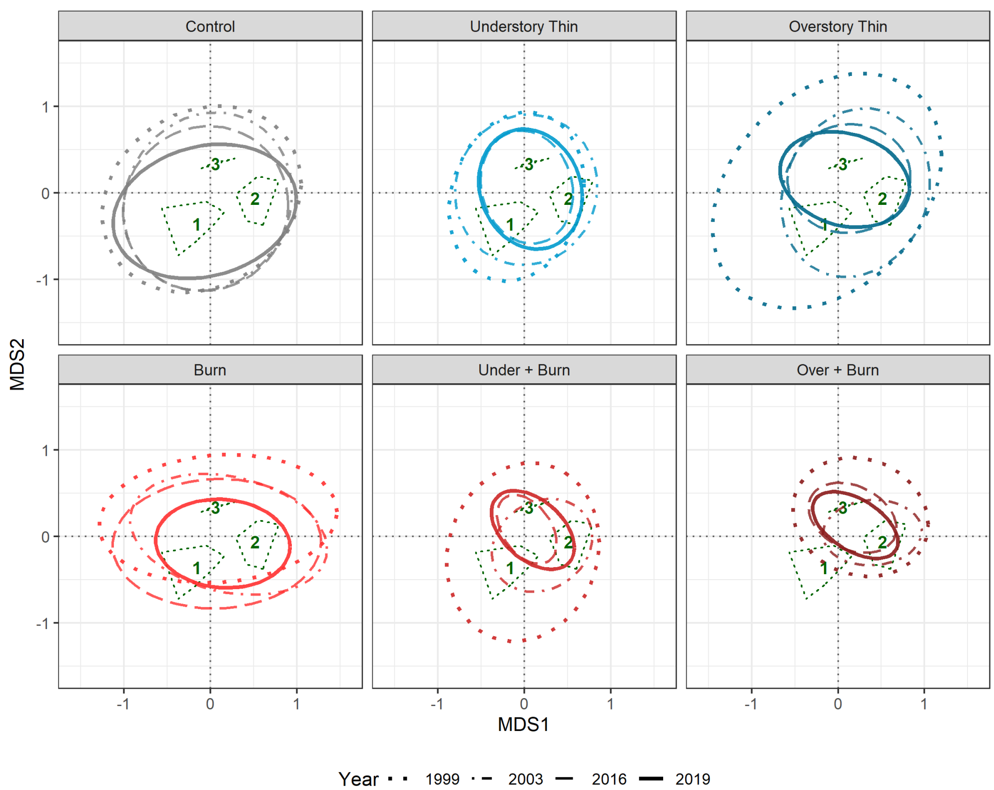
Control
Understory Thin
Overstory Thin
Burn
Under + Burn
Over + Burn
MDS1
MDS2
Year
1999
2003
2016
2019

Figure 4. NMDS ordination of understory plant communities by treatments before and after initial treatments, 16 years after treatments, and 2 years after following reentry burn treatments in burn plots. This ordination includes the 34 plant species that occurred in at least 2% of sub-plot year combinations. (A) Arrows and dashed lines represent significant environmental variable loadings for the ordination (p < 0.005). Green text and polygons signify indicator plant species for three different plant communities previously identified at TEF (North et al. 2005). Points connected by lines indicate the trajectories of treatment centroids through the ordination space over time, with colors and shapes indicating different treatments, and larger points indicating more recent years. (B) Ellipses represent 95% of the distribution of understory communities for each treatment-year combination. Green polygons represent the three plant community types from (A). Smaller ellipses indicate less dispersion of local understory communities from the centroid (i.e. more homogeneous understory communities between sites) for within the treatment-year.

After initial treatment in 2001, thin-burn treatments had significantly more homogenous understory communities than the control, and the overstory thin-burn treatment was significantly more homogenous than all other treatments (thin-burn and thin-only treatments shifted towards diverse herb-dominated communities characterized by high bare ground at that time (Figure 4.). By 15 years following initial treatment, all thin-burn and thin-only treatments experienced increased homogeneity and shifted toward shrub communities dominated by *Ceanothus cordulatus* and *Arctostaphylos patula*. Both thin-burn treatments had significantly more homogenous understory communities than other treatments. The second burn treatment in 2019 did not substantially alter the homogeneity or overall community composition for either thin-burn treatment.

The burn-only treatment did not experience significant homogenization or shift towards heavy herbaceous or shrub cover following initial treatment or during the subsequent 15 years. After the second burn treatment, it experienced a smaller homogenization of the understory plant community and shift toward the herb-dominated community common to other burn treatments following the first burn. However, it remained significantly more heterogenous than the thin-burn treatments.

Environmental conditions, particularly canopy/light environment, substrate, and water strongly influence understory plant community composition (Figure 4). Low light and high litter are characterized by a mixed community of shade-tolerant herbs and shrubs (community 1). High bare ground is characterized by a number of herbaceous species that typically occur at low coverage (community 2). High light, low moisture, and high heat loads are characterized by high shrub cover (community 3). A full description of these communities and indicator species can be found in North et al. (2005).

3.3. Fire and environmental characteristic influence on understory community response

Fire did not uniformly impact plots within the burn treatments, and the two burn events showed very different patterns of fire across treatments. The understory thin-burn treatment experienced noticeable fire (≥ 1% ground cover of ash and char) at 72% of sub-plots in 2001, and only 19% of subplots in 2017. Similarly, the overstory thin-burn treatment experienced noticeable fire at 76% of sub-plots in 2001, and only 24% of subplots in 2017. In contrast, The burn-only treatment only experienced noticeable fire at only 25% of sub-plots in 2001 and 36% in 2017. The initial burn treatment in 2001 burned extensively in the thinned plots, with little effect on the un-thinned plots, while the opposite pattern is true in the second prescribed burn event in 2017.

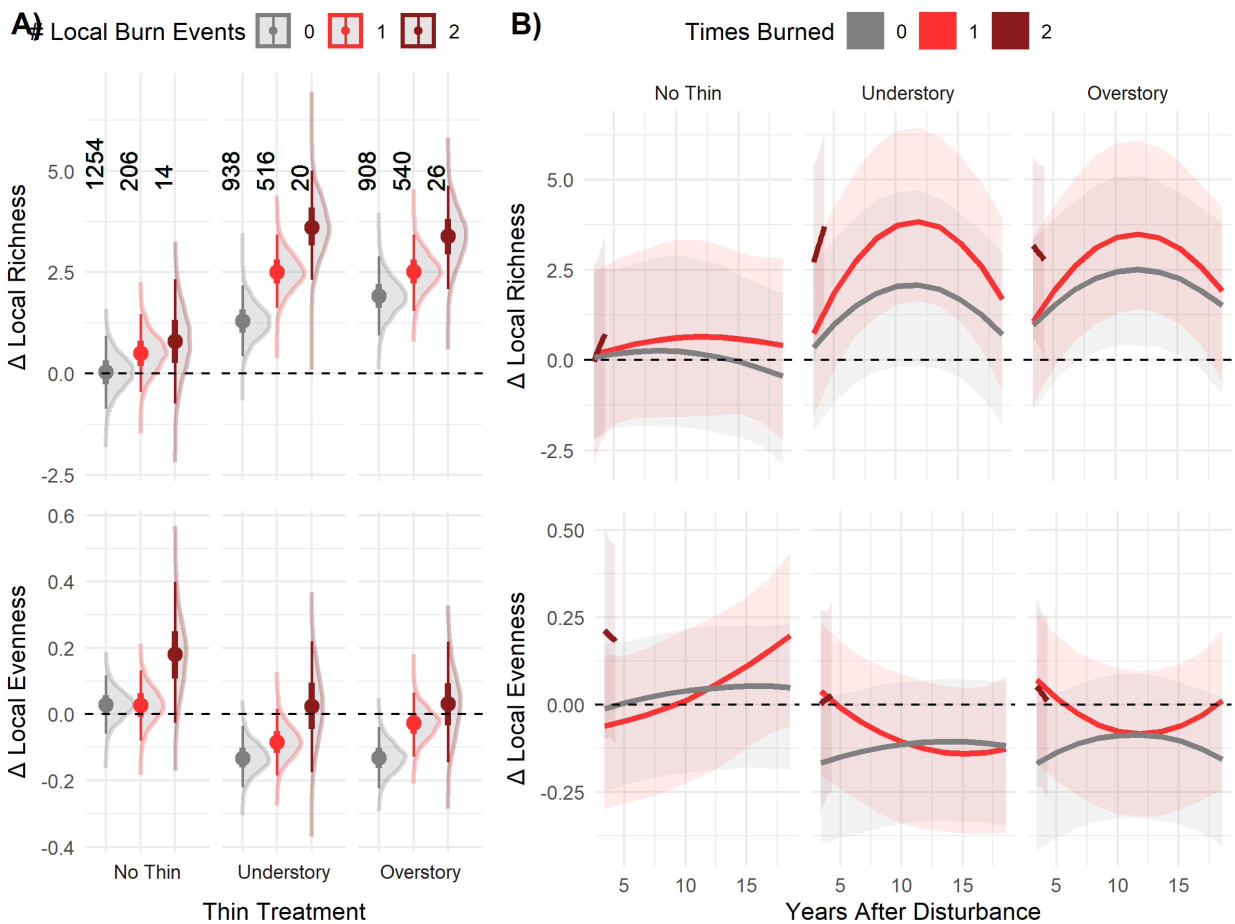

Figure 5. A) Posterior draws of estimated marginal means from a Bayesian hierarchical model of change in local understory plant richness and evenness as a function of thinning treatment and number of burn events, with random effects for plot and year. Points and intervals indicate median and 50% and 95% credible intervals for model fits for each treatment. Shaded areas indicate distributions of posterior linear predictions for each. Number of data points in each group is indicated in black. B) Fitted draws from the joint posterior distribution of a Bayesian hierarchical model of change in local understory plant richness and evenness as a function of thinning treatment, number of burn events, and time since disturbance, with random effects for plot and year. Lines and shaded areas indicate median and 95% credible intervals for model fits for each treatment over time.

Draws from the joint posterior distribution of our hierarchical Bayesian models indicate that richness and evenness responded differently to thinning and burning (Figure 5a). Contrasts of model-estimated marginal means of linear predictions for the effect of burn number and thinning treatment on richness, evenness, and diversity in the 2 – 18 year period following initial treatment indicate that experiencing one fire is more likely to result in more positive change in local richness than no fire, and the effect is greater in areas that were thinned ($p = 0.0077$ for no thin, $p < 0.0001$ for understory thin, and $p = 0.001$ for overstory thin). The small number of locations that experienced two burns in each level of thinning showed greater increases in richness than their unburned and once-burned counterparts. Thinning resulted in a more negative change in evenness ($p = .0073$ for understory thin and $p = .013$ for overstory thin), but one or two burn events reduce this effect and there was little difference between levels of thinning.

Taking time since disturbance into account, thin treatments with and without fire have a clear non-linear effect on richness over time, peaking ~12 years after disturbance (Figure 5b). Regardless of initial thin treatment, burning led to at least a small increase in richness relative to unburned sub-plots. This effect was minor in the un-thinned treatment, and strongest in the understory thin treatment. Evenness decreased following thin treatments, and remained low over time. Burned areas had little change in evenness initially, regardless of thin treatment, but those in thinned treatments lost evenness over time. The burned un-thinned locations maintained their evenness over time. While it is too early after the second fire to determine richness and evenness trajectories, a second burn event at the local scale has led to at least a temporary increase in both richness and evenness across thinning treatments.

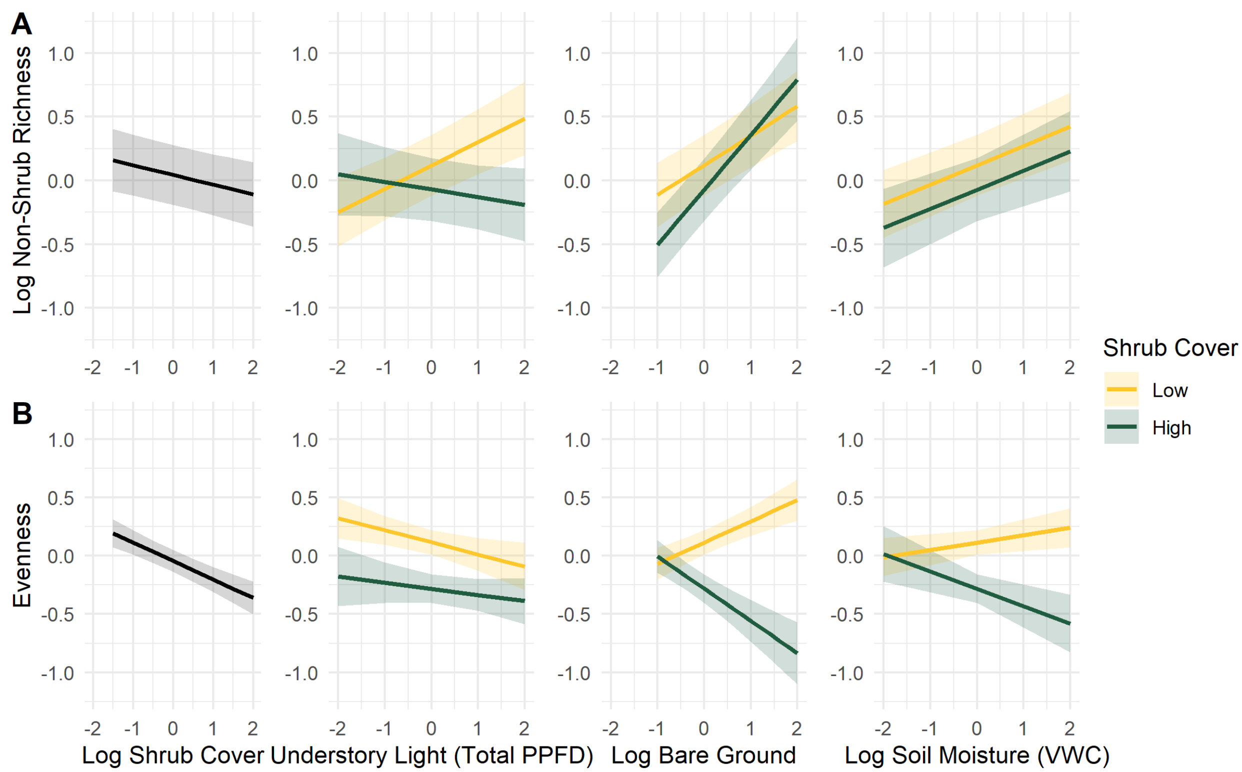

Figure 6. Predicted marginal effects of shrub cover and environmental factors on local A) understory non-shrub richness, and B) evenness, with 95% confidence intervals. Richness, shrub cover, bare ground, and soil moisture are log transformed, and all response and predictor variables are centered to the mean and scaled by standard deviation.

Richness and evenness show different responses to environmental conditions, and plant diversity response to environmental conditions is heavily influenced by shrub cover. Local non-shrub richness and evenness are both maximized under high bare ground and soil moisture with low shrub cover (Figure 6). Evenness is negatively associated with high shrub cover. Available light's effect on non-shrub richness is dependent on shrub cover, as are the effects of bare ground and soil moisture on evenness. Additional understory light only increases richness with low shrub cover, while additional bare ground can increase evenness under low-shrub conditions, and decrease it under high shrub conditions.

3.4. Comparing experimental outcomes with frequent-fire forests.

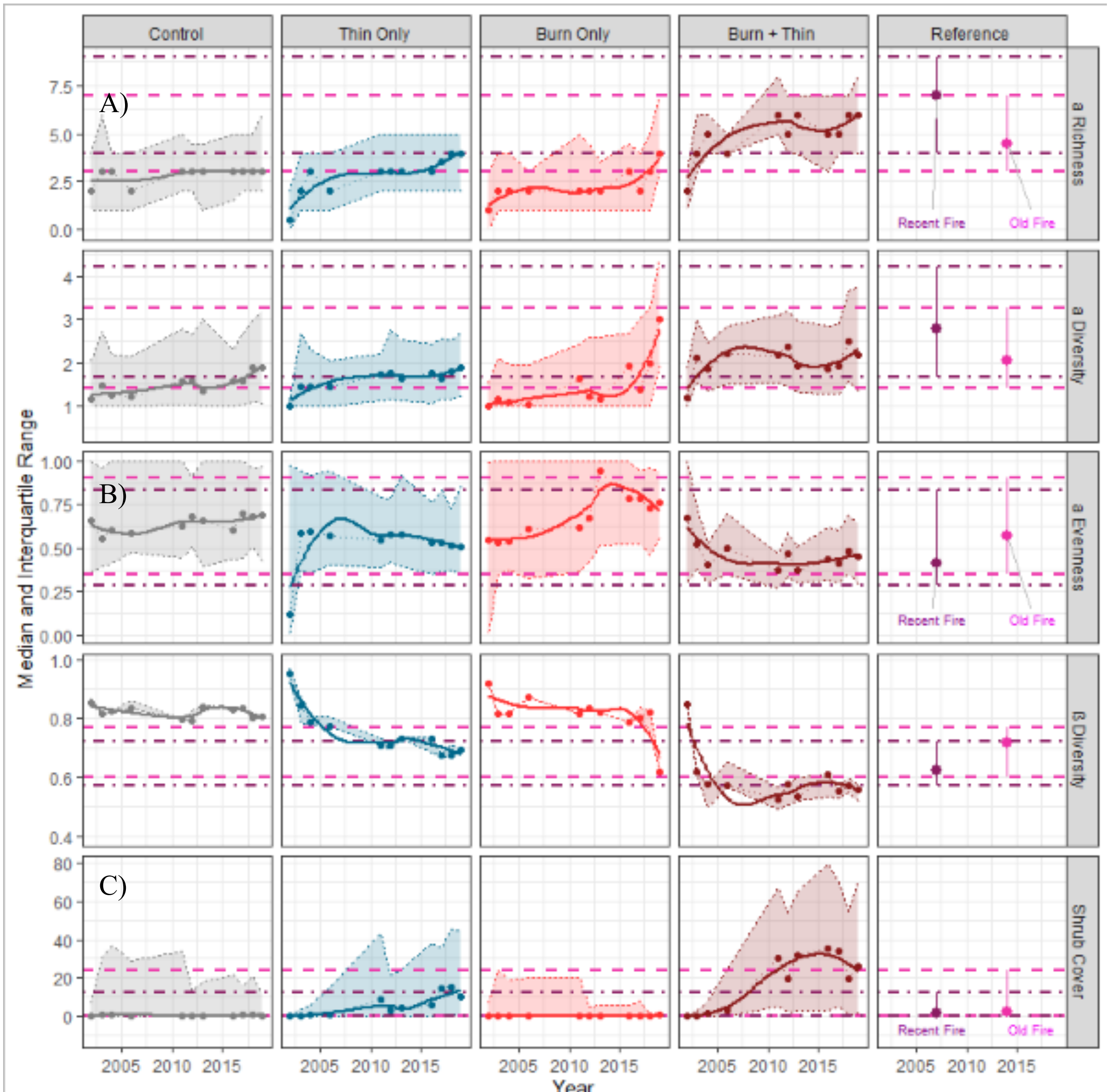

Figure 7. Median and interquartile ranges over time for (top to bottom) a) local richness, b) local diversity, c) local evenness, d) β diversity, and e) shrub cover in experimental treatments in Teakettle Experimental Forest and frequent-fire forests with recent (2-7 years ago) and older (13-20 years ago) fires. For this figure, the thinning treatments at TEF have been combined to facilitate comparison with

the reference conditions. Points represent median values in each year, bold lines represent a smoothed trend in median over time (Loess smoothing function, median ~ year), and colored areas represent the middle 50% of values for each year. Horizontal dashed lines represent the 25th and 75th percentile of values for frequent-fire sites with more recent and older fires for comparison to TEF treatments.

We found that sampled old-growth mixed-conifer forests with frequent fire regimes (hereafter "reference forests") were typically more species rich at the local level (Figure 7a) than fire-suppressed control forests at TEF, but with similar evenness (Figure 7c), leading to higher local diversity (Figure 7b). They also had lower beta diversity than fire-suppressed control forests (Figure 7d), and similar levels of shrub cover Figure 7e). Thin-burn treatments did approximate richness in reference forests initially following treatment, but with reduced evenness and beta diversity. Shrub cover in thin-burn treatments roughly approximated recently burned reference forests for a few years, but rapidly increased to levels much higher than reference forests after 10 years post-treatment. Thin-only and burn-only treatments did not reach richness levels typical of reference forests at any point in the 16 years following initial treatment. However, the burn-only treatment did roughly match the local diversity and evenness and beta diversity of recently burned reference forests in the years following a second burn event.

Frequent-fire forests with more recent fires (3-7 years old) showed higher local richness and diversity, but somewhat lower evenness, beta diversity, and shrub cover than sites with older fires (13-20 years old). This is in contrast to our thin-burn treatments, which show declining evenness and beta diversity over time.

4. Discussion

This study points to key differences in how treatment affects plant understory diversity.

Although local understory plant richness initially increased most following thinning combined with prescribed fire, this fuels reduction treatment did not generate understory communities similar to those in reference old-growth, mixed-conifer forests with frequent, low severity fire regimes. Intense growth of shrubs after thinning, and especially thinning followed by fire (Goodwin et al. 2018), resulted in low understory evenness and beta diversity over time, which a secondary burn treatment emulating the historic fire return interval did not alter. High, continuous shrub cover created a fuelbed prone to either no burning or complete consumption, both of which may entrench current shrub conditions. High shrub response may be driven by fire's stimulation of seed germination and resprouting, and augmented by thinning's reduction in live tree basal area which reduced competition for light, belowground water, and nutrients (Goodwin et al. 2018, Halpern 1989). In contrast, burning without thinning retained a more heterogeneous understory over time and, at least in the two years following the second burn treatment, has responded to multiple burns with high understory richness and evenness, conditions more similar to reference forest understories. In this treatment, low levels of shrub cover created by dispersed, discrete patches actually increased understory evenness and created more variable fire effects. Our results suggest management treatments may need to focus on creating heterogeneity not only in burn effects but also in environmental conditions to foster diverse forest understories and limit shrub cover.

This study has several limitations to consider when interpreting our results. First, replication can be limited in this type of large-scale field experiment, resulting in low statistical power for comparing plot-level metrics. We try to address this limitation by using hierarchical models that take advantage of the nested structure of our study design. Second, reference sites for mixed-conifer forests with intact or restored fire regimes are rare (Lydersen and North 2012) and pose challenges for relevant understory comparisons because individual species may or may not be shared in species pools across locations. We attempted to address this limitation by selecting reference sites as similar as possible to TEF conditions (elevation, slopes, aspects, overstory composition, same dominant shrub species). We also limit our use of reference site comparisons to define a range of variation for mid-elevation mixed-conifer forest stands with what is often considered target conditions for forest restoration treatments. Third, we have limited data following the second burn, and we saw from the initial treatments that there is a strong temporal component to understory response. We can only compare the initial effects of the second burn, and we expect that the effects will continue to change over time.

Local richness, local evenness, and beta diversity showed conflicting trends in our study, indicating that many of the sites that gained species locally following thinning and prescribed fire also became more dominated by a small subset of similar species across sites. Other studies have also suggested different metrics of diversity frequently show divergent responses to disturbance, even when presenting the results from the same experiment (Li et al. 2004, Svensson et al. 2012). Similarly, different richness responses at different spatial scales in our study indicate that burning and thinning have allowed more species to coexist within particular microsites, but have not altered the stand-level richness due to more shared species between those microsites.

Understory community response varied greatly between the first and second burn events, likely due to different fire behavior in 2001 and 2017. The second burn only had a major response in the un-thinned treatment, and very little effect in the two thinned treatments. We suspect that this may be due to cool, high humidity conditions during the burn and high moisture in shrubs dampening combustion. However, sub-plots that did experience more fires (0<1<2) did show signs of increased local richness and evenness (Figure 5a), indicating that we only see the effect in the burn-only plots because so few of the subplots in the thin-burn treatments actually burned in the second fire. This difference in burn behavior often occurs between repeated prescribed fire applications (Waring et al. 2016) and highlights how variable second-entry fire can be due to fuel loading and shrub response following the first burn. Compounding these effects, fuels were elevated in the burn/no thin plots because mortality from California's 2012-2016 drought was higher in these stands due to their higher density (Steel et al. In review). Our results suggest that for managed forests where prescribed burning is often cautiously applied, understory restoration may require more time and repeated burning.

Understory plant community response had a strong temporal component following thinning and prescribed fire, with local richness peaking ~10-12 years after thin-burn treatments, and evenness and beta diversity declining in the first several years following burning and thinning (Figure 7). This pattern appears to align with the historic fire return interval in Sierran mixed-conifer forest (van de Water and Safford 2011, Safford and Stevens 2017). Fine-scale plant diversity is also maximized under the environmental conditions expected shortly after a low-moderate severity fire, or in a burn with thinning: a high light environment with available substrate for seeds and low shrub cover that might block light or compete for space, water, and nutrients. Early results published from the TEF understory study emphasize that thinning may be necessary prior to burning to produce a strong herbaceous response (Wayman and North 2007). However, later results emphasize a heavy shrub response 5-10 years following thin-burn and thin treatments (Goodwin et al. 2018). Given the important temporal dimension of understory response to disturbance, understanding the full effect of our second burn treatment will require continued study.

The observed trends in understory community diversity after initial treatment in this study are correlated with the growth of shrubs as an understory dominant and a shift toward open shrub-dominated community types over ~10 – 12 years following thinning and burning. Other studies of understory communities and shrub cover have found shrubs to be a major driver of understory plant richness and diversity after wildfires over a multi-decade temporal scale (Bohlman et al. 2016, Webster and Halpern 2010). This large increase in shrub cover in our thin-burn treatments may be analogous to conditions following wildfires in similar mixed-conifer forests, where high severity fire and shrub cover can create a positive feedback loop that induces type conversion from conifer forest to an alternate stable state of montane chaparral (Coppoletta et al. 2016). Results from TEF's thin-burn treatments agree with a recent analysis of understory diversity in Sierra Nevada yellow pine and mixed-conifer forests following different fire severities, in which moderate - high severity patches (>50-75% basal area mortality) had the highest richness and diversity, but evenness and beta diversity declined with greater fire severity, with fire-stimulated *Ceonothus cordulatus* as an indicator species for moderate-high severity fire (Richter et al.). Despite relatively low levels of crown scorch in initial burn treatments compared to a high severity wildfire(Innes et al. 2006), thin-burn treatments may emulate high-severity burn conditions by releasing shrubs from competition with trees while stimulating their abundant soil-banked seed and sprouting from fire (Halpern 1989, Huffman and Moore 2004).

Across our reference sites, age of the most recent fire influenced local richness, evenness, and diversity, and beta diversity (Figure 7). Although shrub cover is higher in reference forests with older fires, we found median shrub cover to be near zero indicating that shrubs remain concentrated in discrete patches rather than widespread. Although thin-burn treatments increased local richness and diversity the most following initial treatment, they only briefly approximate recently burned reference forests and quickly diverge. Their lower evenness and beta diversity and considerably higher shrub cover do not closely match conditions in reference forests with older fires.

Patchiness within prescribed fire treatments may be beneficial to maintaining diverse understories across larger spatial scales. Congruent with other studies of understory plant community response to fire in mixed-conifer forests, more intensive patches of fire maximize benefits to local richness in areas with reduction in litter and increases in light availability, while temporarily reducing shrub cover. While these treatments became more homogeneous at the four-ha plot scale over time, spatial and temporal variability in fire behavior may maintain beta diversity in the landscape by retaining closed, mesic understory community. Such heterogeneity in fire history could support a greater phylogenetic plant diversity by increase abundance and richness of plants from the southern-xeric biogeographic affinity in local patches while providing habitat refugia for plants from north-temperate biogeographic affinity (Stevens et al. 2015). This also fits with the recently proposed framework that increased pyrodiversity, or diversity of fire histories, at the landscape scale supports increased biodiversity (He et al. 2019).

4.1 Management Implications

Conversion from mixed-conifer forest to shrub-field communities is an undesirable outcome of high severity wildfire for many forest managers in the Sierra Nevada, and would be an unintended outcome for forest restoration and fuels reduction treatments designed to reduce the risk of high-severity fire in these forests. A previous understory analysis in the TEF found shrub cover positively correlated with reduction in live tree basal area associated with thinning and subsequent mortality in the 2012 -2015 drought (Goodwin et al. 2018).

Restoring understory conditions may not happen after a single prescribed burn, regardless of initial thinning. Our results are in agreement with long-term monitoring of understory response to multiple fires in mixed-conifer forests in Sequoia and Kings Canyon National Parks, where understory plant diversity responses often needed long time periods (10 – 20 years) after fire or even multiple fire events to become fully apparent (Webster and Halpern 2010). Restoring the understory conditions and plant communities in fire-suppressed mixed-conifer forests may take multiple treatments over many years.

Literature Cited

1. Abella, S. R. & Springer, J. D. Effects of tree cutting and fire on understory vegetation in mixed conifer forests. *Forest Ecology and Management* **335**, 281–299 (2015).
2. Baldwin, B. G. *et al. The Jepson manual: vascular plants of California*. (Univ of California Press, 2012).
3. Bates, D., Mächler, M., Bolker, B. M. & Walker, S. C. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, (2015).
4. Beers, T. W., Dress, P. E. & Wensel, L. C. Notes and observations: aspect transformation in site productivity research. *J. For.* **64**, 691–692 (1966).
5. Bohlman, G. N., North, M. & Safford, H. D. Shrub removal in reforested post-fire areas increases native plant species richness. *For. Ecol. Manage.* **374**, 195–210 (2016).
6. Bürkner, P.-C. {brms}: An {R} Package for {Bayesian} Multilevel Models Using {Stan}. *J. Stat. Softw.* **80**, 1–28 (2017).
7. Coppoletta, M., Merriam, K. E. & Collins, B. M. Post-fire vegetation and fuel development influences fire severity patterns in reburns. *Ecol. Appl.* **26**, 686–699 (2016).
8. Fettig, C. J., Mortenson, L. A., Bulaon, B. M. & Foulk, P. B. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. *For. Ecol. Manage.* **432**, 164–178 (2019).
9. Fiegener, R. P. The influence of sampling intensity on the fire history of the Teakettle Experimental Forest, Sierra Nevada, California: small fire detection, the composite fire chronology, and fire interval calculation. (2002).
10. Goodwin, M. J., North, M. P., Zald, H. S. J. & Hurteau, M. D. The 15-year post-treatment response of a mixed-conifer understory plant community to thinning and burning treatments. *For. Ecol. Manage.* **429**, 617–624 (2018).
11. Halpern, C. B. Early Successional Patterns of Forest Species: Interactions of Life History Traits and Disturbance. *Ecology* **70**, 704–720 (1989).
12. He, T., Lamont, B. B. & Pausas, J. G. Fire as a key driver of Earth's biodiversity. *Int. J. Wildl. Fire* **3**, 1983–2010 (2019).
13. Horwitz, W. *Official methods of analysis of AOAC International. Volume I, agricultural chemicals, contaminants, drugs/edited by William Horwitz.* (Gaithersburg (Maryland): AOAC International, 1997., 2010).
14. Huffman, D. W. & Moore, M. M. Responses of Fendler ceanothus to overstory thinning, prescribed fire, and drought in an Arizona ponderosa pine forest. *For. Ecol. Manage.* **198**, 105–115 (2004).
15. Jost, L. Entropy and diversity. *Oikos* **113**, 363–375 (2006).
16. Koontz, M. J., North, M. P., Werner, C. M., Fick, S. E. & Latimer, A. M. Local forest structure variability increases resilience to wildfire in dry western U.S. coniferous forests. *Ecol. Lett.* **23**, 483–494 (2020).

17. Lenth, R. emmeans: Estimated Marginal Means, aka Least-Squares Means. (2020).

18. Li, J. *et al.* Issues Affecting the Measurement of Disturbance Response Patterns in Herbaceous Vegetation : A Test of the Intermediate Disturbance

19. Lüdecke, D. ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *J. Open Source Softw.* **3**, 772 (2018).

20. Lydersen, J. & North, M. Topographic Variation in Structure of Mixed-Conifer Forests Under an Active-Fire Regime. 1134–1146 (2012). doi:10.1007/s10021-012-9573-8

21. Ma, S., Concilio, A., Oakley, B., North, M. & Chen, J. Spatial variability in microclimate in a mixed-conifer forest before and after thinning and bu

22. North, M. *et al. Vegetation and Ecological Characteristics of Mixed-conifer and Red Fir Forests at the Teakettle Experimental Forest*. (2002).

23. North, M., Oakley, B., Fiegener, R., Gray, A. & Barbour, M. Influence of light and soil moisture on Sierran mixed-conifer understory communities. *Plant Ecol.* **177**, 13–24 (2005).

24. Oksanen, J. *et al.* vegan: Community Ecology Package. (2019).

25. Olsen, S. R. & Sommers, L. E. Phosphorus. p. 403–430. AL Page et al.(ed.) Methods of soil analysis. Part 2. Agron. Monogr. 9. ASA and SSSA, Madison, WI. *Phosphorus. p. 403–430. AL Page al.(ed.) Methods soil Anal. Part 2. 2nd ed. Agron. Monogr. 9. ASA SSSA, Madison, WI.* (1982).

26. Potter, D. A. *Forested Communities of the Upper Montane in the Central and Southern Sierra Nevada*. (1998).

27. Raup, D. M. & Crick, R. E. Measurement of faunal similarity in paleontology. *J. Paleontol.* 1213–1227 (1979).

28. Richter, C. *et al.* The species diversity × fire severity relationship is hump-shaped in semiarid yellow pine and mixed conifer forests. *Ecosphere* **10**, (2019).

29. Safford, H. D., Stevens, J. T., Merriam, K., Meyer, M. D. & Latimer, A. M. Forest Ecology and Management Fuel treatment effectiveness in California yellow pine and mixed conifer forests. *For. Ecol. Manage.* **274**, 17–28 (2012).

30. Safford, H. D. & Stevens, J. T. *Natural Range of Variation for Yellow Pine and Mixed-Conifer Forests in the Sierra Nevada, Southern Cascades, and Modoc and Inyo National Forests, California, USA*. (2017).

31. Service, F. *et al.* An Ecosystem Management Strategy for Sierran Mixed- Conifer Forests. (2009).

32. Sheldrick, B. H. & Wang, C. Particle size distribution. pp: 499–511. *MR Cart.* (1993).

33. Shevock, J. R. *Status of rare and endemic plants. Sierra Nevada Ecosystem Project, Final Report to Congress, vol. II. Assessments and Scientific Basis for Management Options.* (1996).

34. Smith, T. F., Rizzo, D. M. & North, M. Patterns of Mortality in an Old-Growth Mixed-Conifer Forest of the Southern Sierra Nevada, California. *For. Sci.* **51**, 266–275 (2005).

35. Stevens, J. T., Safford, H. D., Harrison, S. & Latimer, A. M. Forest disturbance accelerates thermophilization of understory plant communities. doi:10.1111/1365-2745.12426
36. Svensson, J. R., Lindegarth, M., Jonsson, P. R. & Pavia, H. Disturbance-diversity models: what do they really predict and how are they tested? *Proc. R. Soc. B Biol. Sci.* **279**, 2163–2170 (2012).
37. ter Steege, H. Hemiphot.R: Free R scripts to analyse hemispherical photographs for canopy openness, leaf area index and photosynthetic active radiation under forest canopies. (2018).
38. Van De Water, K. M. & Safford, H. D. A summary of fire frequency estimates for California vegetation before Euro-American settlement. **7**, (2011).
39. Verner, J. *et al. The California Spotted Owl: A Technical Assessment of Its Current Status*. (1992).
40. Wayman, R. B. & North, M. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. *For. Ecol. Manage.* **239**, 32–44 (2007).
41. Webster, K. M. & Halpern, C. B. Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. *Ecosphere* **1**, art9 (2010).
42. Zald, H. S. J., Gray, A. N., North, M. & Kern, R. A. Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest, USA. *Elsevier* doi:10.1016/j.foreco.2008.04.022

Appendices.

Appendix 1. summary statistics of diversity metrics, cover, and environmental variables across treatments and years. Different letters following means denote significant differences (adjusted p < 0.05) between treatments for a given year (Dunn's post hoc analysis of the Kruskal-Wallis Test, with Bonferroni correction for multiple pairwise comparisons). Different numbers following means denote significant differences between years (adjusted p < 0.05, Wilcoxon's post-hoc analysis of the Friedman Test, with Bonferroni correction for multiple pairwise comparisons).

Metric	Year	Control	Understory Thin	Overstory Thin	Burn-Only	Burn + Understory Thin	Burn + Overstory Thin
α Richness mean (s.d.)	1999	3.45 (3.48) a	2.90 (2.97) ab 1	2.01 (2.38) b 1	2.39 (2.17) ab 1	2.90 (2.50) ab 1	2.24 (1.92) ab 1
	2003	4.04 (4.14) ab	3.37 (3.48) ab 1	2.90 (3.25) a 2	3.13 (2.88) a 2	5.31 (3.29) c 2	4.04 (1.97) bc 2
	2016	3.33 (2.39) a	3.99 (2.30) ab 2	3.06 (2.49) a 2	3.19 (2.26) a 2	5.94 (3.03) c 23	4.51 (2.20) bc 2
	2019	4.15 (3.13) a	4.21 (2.61) a 2	4.07 (2.70) a 3	5.10 (3.08) ab 3	6.49 (3.56) b 3	6.06 (2.93) b 3
α Diversity (Effective Species) mean (s.d.)	1999	1.86 (1.24) 1	1.82 (1.17) 1	1.58 (1.29) 1	1.62 (1.09) 1	1.80 (1.10) 1	1.67 (0.93) 1
	2003	2.32 (2.03) ab 23	2.05 (1.50) ab 12	2.08 (1.58) a 2	1.79 (1.13) a 12	2.42 (1.12) b 2	2.28 (1.03) b 23
	2016	2.00 (1.20) ab 12	1.97 (0.90) ab 12	2.00 (1.25) a 2	2.26 (1.63) ab 2	2.61 (1.68) b 2	2.04 (1.21) ab 12
	2019	2.70 (2.10) a 3	2.20 (1.33) a 2	2.05 (1.05) a 2	3.41 (1.87) b 3	2.79 (1.83) ab 2	2.85 (1.93) ab 3
β Richness (Raup-Crick Dissimilarity) mean (s.d.)	1999	0.84 (0.01) ab 1	0.81 (0.04) a 1	0.89 (0.02) c 1	0.86 (0.05) d 1	0.87 (0.02) d 1	0.86 (0.05) bd 1
	2003	0.81 (0.00) ab 2	0.80 (0.03) a 2	0.86 (0.03) c 2	0.82 (0.04) bc 2	0.66 (0.08) d 2	0.62 (0.03) e 2
	2016	0.84 (0.02) a 3	0.69 (0.02) b 3	0.79 (0.10) c 3	0.78 (0.06) c 3	0.57 (0.07) d 3	0.61 (0.02) d 3
	2019	0.79 (0.04) a 4	0.71 (0.03) b 4	0.69 (0.01) b 4	0.64 (0.04) c 4	0.54 (0.04) d 4	0.56 (0.01) d 4
Boostrap γ Richness mean (s.d.)	1999	66.41 (23.46) a 1	27.50 (7.03) b 1	42.48 (16.48) c 1	29.01 (4.46) b 1	39.25 (7.46) c 1	28.10 (9.42) b 1
	2003	76.25 (29.61) a 2	31.65 (5.50) b 2	48.92 (18.67) c 2	36.27 (7.60) b 2	42.18 (4.00) ac 2	26.99 (5.66) d 1
	2016	55.93 (19.89) a 3	31.45 (5.02) b 2	43.78 (18.18) a 3	34.37 (8.64) c 3	40.12 (5.17) a 1	32.20 (5.25) bc 2
	2019	60.78 (18.53) a 4	33.90 (7.08) b 3	42.41 (13.73) c 1	42.80 (11.78) c 4	45.57 (6.03) c 3	33.96 (3.07) b 3
Total % Plant Cover mean (s.d.)	1999	29.51 (35.56) a 1	19.06 (28.34) ab 12	14.42 (32.51) b 12	25.71 (31.65) a 1	22.27 (40.21) ab 1	18.35 (28.91) ab 1
	2003	25.99 (31.25) a 1	14.29 (21.64) ab 1	7.90 (17.28) b 1	22.22 (25.51) a 1	23.89 (25.62) a 1	20.70 (27.46) a 1
	2016	17.39 (27.02) a 2	29.14 (29.95) b 2	18.92 (28.49) a 2	10.07 (18.37) a 2	47.54 (35.70) b 2	42.26 (37.05) b 2
	2019	12.43 (17.31) a 2	28.19 (30.71) bc 2	27.14 (30.67) b 3	8.75 (14.11) a 2	42.15 (33.35) c 2	39.55 (33.74) bc 2
% Shrub Cover mean (s.d.)	1999	20.96 (30.93)	16.61 (27.75) 12	12.52 (30.96) 12	23.30 (32.67)	19.19 (40.41) 1	17.19 (29.30) 1
	2003	16.26 (25.27)	9.32 (19.54) 1	3.52 (10.45) 1	14.36 (24.71)	7.36 (15.37) 1	4.02 (9.82) 2
	2016	14.08 (25.40) a	26.79 (30.69) bc 2	16.65 (27.01) ab 2	8.83 (18.37) a	42.90 (36.93) c 2	40.24 (38.17) c 3
	2019	8.35 (14.20) a	26.16 (31.22) b 2	24.87 (30.36) b 3	4.79 (13.09) a	36.23 (34.42) b 2	35.83 (35.31) b 3
% Herbaceous Plant Cover mean (s.d.)	1999	1.65 (4.76) a 12	0.46 (1.08) ab 1	0.38 (1.87) b 1	0.69 (1.63) ab 1	1.36 (3.69) ab 1	0.85 (1.75) ab 1
	2003	2.30 (5.20) a 3	2.44 (7.97) a 2	1.89 (6.18) a 2	6.44 (14.19) a 2	13.45 (19.73) b 2	14.25 (25.05) b 2
	2016	0.61 (1.12) ab 1	0.79 (1.43) ab 12	0.59 (1.88) a 12	0.66 (1.44) ab 1	2.63 (4.80) c 3	1.39 (2.52) bc 1
	2019	0.76 (1.22) a 2	0.66 (1.17) a 12	0.72 (1.26) a 2	2.50 (4.81) ab 2	3.26 (4.35) b 3	2.55 (3.97) b 3
% Graminoid Cover mean (s.d.)	1999	0.60 (3.74) a	0.38 (2.44) b 1	0.47 (3.66) a	0.03 (0.14) a	0.55 (1.84) b	0.02 (0.06) ab 1
	2003	0.11 (0.34) a	0.04 (0.26) a 2	0.35 (1.85) a	0.16 (0.99) a	1.24 (4.61) b	0.14 (0.44) a 12
	2016	0.11 (0.75) a	0.38 (0.96) b 1	0.05 (0.21) a	0.01 (0.03) a	0.67 (2.12) b	0.25 (1.24) a 12
	2019	0.25 (1.83) a	0.23 (0.55) b 1	0.05 (0.16) ac	0.03 (0.09) a	0.39 (1.15) b	0.19 (0.65) bc 2
% Bare Ground Cover mean (s.d.)	1999	3.00 (12.70) ab 1	2.26 (14.07) a 1	2.24 (11.14) a 1	4.48 (13.82) ab 1	2.91 (11.99) a 1	13.78 (26.92) b 1
	2003	7.82 (16.54) a 2	14.66 (25.84) a 2	11.61 (22.72) a 2	17.00 (25.00) a 2	38.19 (30.50) b 2	64.36 (27.74) c 2
	2016	2.76 (11.49) a 1	1.67 (6.66) a 1	1.48 (4.30) a 1	1.59 (3.60) ab 1	1.00 (1.78) ab 1	6.37 (14.08) b 1
	2019	7.21 (13.66) a 2	6.58 (13.99) a 2	8.66 (13.44) ab 2	25.94 (23.25) c 3	13.37 (20.25) ab 3	24.57 (26.74) bc 3
Litter Depth (cm) mean (s.d.)	1999	3.53 (3.94) 1	3.98 (3.85) 12	5.02 (4.90)	4.28 (3.98) 1	4.72 (4.91) 1	4.95 (5.29) 1
	2003	3.22 (3.16) ab 1	2.89 (2.82) ab 1	3.61 (3.18) a	1.67 (1.80) b 2	1.77 (1.66) b 2	0.71 (1.14) c 2
	2016	4.90 (4.04) a 2	5.57 (4.94) a 23	4.63 (4.35) a	2.96 (2.01) a 1	2.99 (2.89) a 3	1.77 (1.82) b 3
	2019	4.89 (3.15) a 2	5.44 (3.28) a 3	4.37 (3.19) ab	1.55 (1.63) c 2	3.12 (2.27) bd 13	2.50 (1.96) cd 3
% Coarse Woody Debris Cover mean (s.d.)	1999	9.91 (18.01)	10.57 (18.64) 12	6.34 (12.49) 12	5.57 (11.78)	9.47 (17.41)	7.78 (16.97)
	2003	8.37 (16.57) a	13.19 (20.91) b 1	10.96 (15.89) b 3	4.99 (9.40) a	3.32 (6.68) a	8.78 (14.26) ab
	2016	6.23 (13.50) ab	5.04 (12.06) ab 2	4.56 (8.61) a 1	3.23 (11.39) b	4.08 (13.46) ab	1.55 (2.16) ab
	2019	7.17 (11.19) abc	7.95 (11.01) ab 1	8.85 (12.11) a 23	5.34 (10.60) c	3.28 (4.68) c	3.17 (4.42) bc

Appendix 2. Fire History at Teakettle Experimental Forest. Closed circles represent subplots that experienced noticeable fire effects (>= 1 % ash or char ground cover post-fire). Open circles represent sub-plots that did not experience noticeable fire effects.